SOME RECENT SPECIES OF THE GENUS *ANASKOPORA* WASS, 1975 (BRYOZOA: CRIBRIOMORPHA) FROM QUEENSLAND

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Several species of the genus *Anaskopora* have small, globular colonies, composed principally of frontally budded autozooids, kenozooids and avicularia. Hitherto, all known species have been Tertiary fossils from Victoria. *A. parkeri* sp. nov. is a Recent species here described from the Queensland continental slope. Colonies possess long rhizoids, which are inferred to have also occurred in fossil species with the same mode of growth and colony form. *Cellepora doliaris* Maplestone, 1909, a rare conical species with more regular frontal budding, originally found from New South Wales, has been referred in the past to the genus *Reginella*. It is here redescribed from specimens collected on the continental slope of Queensland, and is reassigned to *Anaskopora*. The characters of the genus *Reginella*, which have been somewhat misunderstood, are discussed and the type species, *R. furcata* (Hincks, 1882), is redescribed. ☐ *Bryozoa, Anaskopora, Reginella, taxonomy, morphology.*

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Colonies of cribriomorph Bryozoa tend to be encrusting and unilaminar, although a few fossil species were inferred to have had a 'free-living' habit.

In this paper, we report the discovery of a new species of deep-sea free-living cribriomorph anchored by rootlets. We place the new species in the genus *Anaskopora*. Wass (1975) revised the genus *Corbulipora* MacGillivray (1895) and described several fossil species from the Victorian Tertiary, some of which he referred to a new subgenus *Anaskopora*. Recent revision of *Corbulipora* has shown that its species occur in multiple growth phases (see Bock & Cook, 1994), and that the species of *Anaskopora* are generically distinct (see Bock & Cook, in press).

The discovery of a Recent species of *Anaskopora* makes a significant contribution to the interpretation of the colony structure of fossil species, several of which can now confidently be inferred to have been anchored by rhizoid systems. Understanding of this mode of growth also allows the inference that the fossil species lived in and upon the upper layers of particulate seabottoms, and were part of a 'sand-fauna' (see Cook, 1981) of similarly adapted bryozoan species.

METHODS

Specimens were bleached in sodium hypochlorite solution and coated with AuPd or carbon for SEM. Abbreviations used: AM, Australian Museum, Sydney; BMNH, Natural History Museum, London; MOV, Museum of Victoria, Melbourne; MTQ, Museum of Tropical Queensland, Townsville; QMG, Queensland Museum, Brisbane.

Morphological terms used in the descriptions are defined in Bassler (1953) and Boardman & Cheetham (1983).

SYSTEMATICS

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATIDA Busk, 1852
Infraorder CRIBRIOMORPHA Harmer, 1926
Family CRIBRILINIDAE Hincks, 1879

Anaskopora Wass, 1975

Anaskopora Wass, 1975:170. Bock & Cook 1996: in press.

TYPE SPECIES. *Cribrilina elevata* MacGillivray, 1895.

DESCRIPTION. Colony encrusting, originating on very small substrata, often globular-to-conical. Autozooids with septulae in the vertical walls, some or all of which become surrounded by a partially calcified chamber with an upper, cuticle-covered window. Zooids budded laterally and distally, or from chambered pores (see below) as interzooidal frontal buds. Interzooidal kenozooids and avicularia, together with rhizoids in some species, produced in the same way. Au-

lozooids with a costate pericyst, with lacunae; pelmatidia rare or absent. Secondary, calcified orifice with paired spines and a raised, distal, fimbriated plate. Avicularia distal or distolateral; occasionally proximal; rostrum rounded or subtriangular, with paired condyles. Ovicells unknown.

The globular species of *Anaskopora*, in particular, possess a kind of pore chamber, here called a 'chambered pore' to distinguish it from other forms of dietellae. This originates as a calcified chamber surrounding one or more septulae in the vertical walls of zooids. The chamber is uncalcified on the frontal side, and the cuticle covering this window is able to expand intussusceptively so that the chamber may enlarge to form interzooidal kenozooids, autozooids, avicularia and rhizoids. Chambered pores occur in *Corbulipora*, but are not the regular source of frontally budded zooids, as they are in the globular species of *Anaskopora*. Some specimens of species described by Bock & Cook (in press), and a few of the colonies of *A. parkeri* (see below), originate upon very small shell substrata. These are rapidly covered by encrusting zooids with chambered pores at their corners. These pores produce an interzooidal, frontally budded series of zooids in subsequent astogenetic generations, which completely supersede any further encrusting growth. In *Anaskopora doliaris*, frontal budding of this kind seems to form the entire colony, and is very regular, so that the conical form is produced.

Anaskopora parkeri sp. nov.
(Figs 1A,B, 2A,B, 3)

MATERIAL EXAMINED. HOLOTYPE: QMG-21282, in alcohol, 'Cidaris 1' Stn 42.2, 17°21.77'S, 146°48.52'E, 15.v.1986, 296-302m, epibenthic sledge (1/2 inch inner liner), at MTQ. PARATYPES: QMG21283, one colony mounted on SEM stub, same data as holotype; QMG21284, one colony mounted on SEM stub, same data as holotype; QMG21285, 56 colonies in alcohol, same data as holotype; MOVF80820, 9 colonies in alcohol, same data as holotype. ADDITIONAL MATERIAL: QMG21288, 71 colonies in alcohol, same data as holotype; QMG21289, 2 colonies in alcohol, 'Cidaris 1' Stn 43.2, 17°34.58'S, 146°53.21'E, 15.v.1986, 458-500m, epibenthic sledge (1/2 inch liner), at MTQ.

ETYMOLOGY. For the late Shane Parker, of the South Australian Museum.

DESCRIPTION. Colonies 0.50-5.0mm in diameter, encrusting small foraminiferans or completely free-living (Fig. 1A), anchored by large rhizoids (Fig. 1B). Autozooids with frontal shield of 18-24 costae alternating with rows of 7-8 lacunae (Fig. 2A). Calcified orifice with one pair of flattened, sometimes terminally bifid, lateral-oral spines (Fig. 2A), paired lateral condyles and a raised distal plate with 5-8 fimbriations (Fig. 2B) and a pit at the base of the outer surface (Fig. 3). Operculum golden-brown, with a marginal sclerite, filling the secondary orifice. Septulae 2-3 distal, 3-4 lateral, becoming surrounded by chambered pores (Fig. 3) which develop frontally as a series of 4-6 small kenozooids with cuticular frontals, surrounding each zooid. Avicularia distolateral (Figs 2A, 3), developed from chambered pores; occasionally paired or even proximal. Subrostral chambers raised, rounded (Fig. 3); mandibles with a marginal sclerite, oriented laterally. Zooids budded in alternating interzooidal series from chambered pores, oriented irregularly, colony forming an ectoproctolith (Figs 1A, 2A, 3). Interzooidal kenozooids becoming extrazooidal.

Colony and zooid dimensions are given in Table 1.

REMARKS. *A. parkeri* closely resembles *A. cornuta* (MacGillivray, 1895), which was referred to *Corbulipora* by Wass (1975) but reassigned to *Anaskopora* by Bock & Cook (in press). The two species have similar colony structures, and the autozooids of *A. cornuta* have numerous straight rows of costae, alternating with small lacunae, like those of *A. parkeri*. *A. cornuta* differs in the distal position of the avicularium, which is not nearly as prominent as that of *A. parkeri*. The two species are so alike that it seems certain that the Victorian Tertiary species was a direct ancestor of the Recent form from Queensland. It may also be inferred with a high degree of confidence that the colonies of *A. cornuta* possessed rhizoids and lived in a similar microenvironment to that inhabited by *A. parkeri*.

Of 75 colonies of *A. parkeri* from Stn 42.2, 20 had well developed rhizoids which were 2-3mm long and, when turgid, 0.33-0.38mm wide. The colonies exhibited a developmental series; the smallest had 6 zooids, the largest approximately 50 autozooids visible at the surface. Where the youngest stages encrusted small foraminifera there was a large, cuticle-covered cavity next to the primary zooid; in two cases, with a large rhizoid beside it. Whether the cuticle-covered cavity is the ancestrula is not known. The rhizoids themselves terminated in numerous rootlets which had shell fragments and foraminiferans adhering to the cuticle. One colony was the substratum for a small colony of a tubuliporid cyclo-

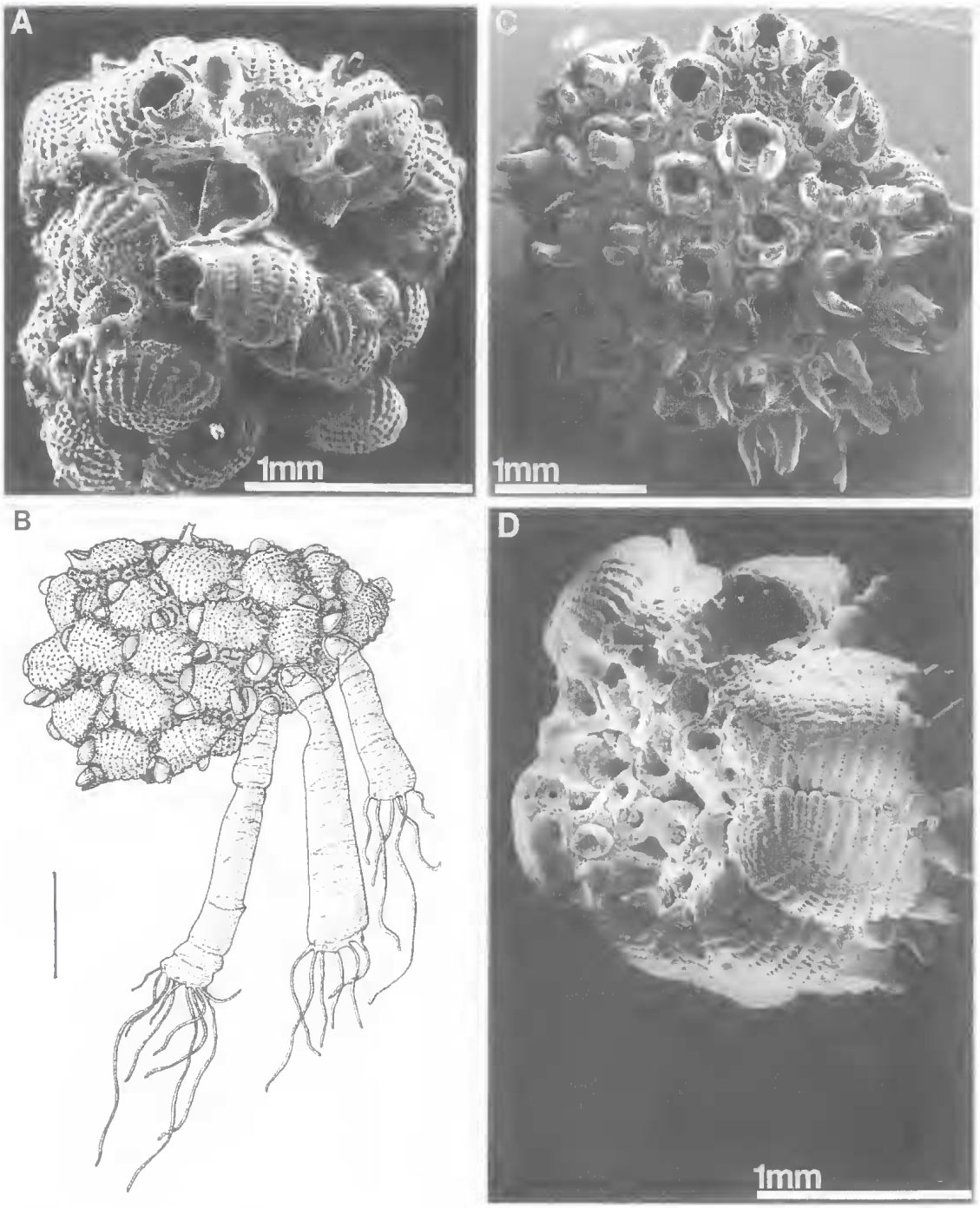

FIG. 1. A-B, *Anaskopora parkeri* sp. nov. A, QMG21283, frontally budded colony, x 32; B, Sketch of colony with rhizoids, x 15. C-D, *A. doliaris* (Maplestone). C, QMG21286, colony from frontal side, x 21; D, QMG21287, colony from basal side, x 31.

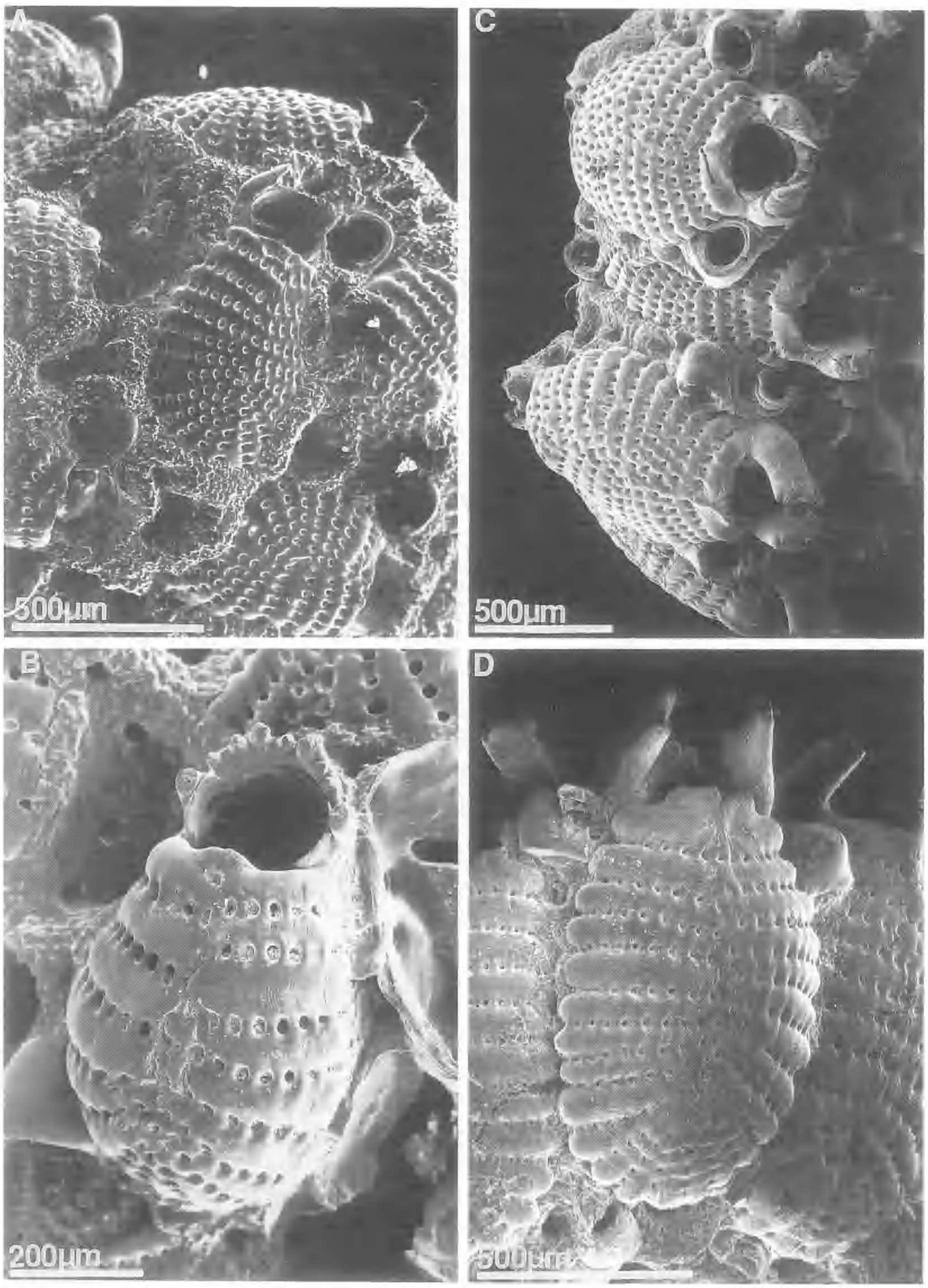

FIG. 2. A-B, *Anaskopora parkeri* sp. nov. A, QMG21284, general view of zooids, x 58; B, QMG21283, enlarged view of one zooid, x 100. C-D, *A. doliaris* (Maplestone). C, QMG21286, general view of zooids, x 42; D, QMG21287, enlarged view of one zooid, x 66.

FIG. 3. *Anaskopora parkeri* sp. nov, QMG21283. Autozooids showing details of orifices and frontal buds, x 37.

stome. Two others had the horny skeleton of *Stephanoscyphus* (Scyphozoa: Coronatae) growing on them; Lagaaij (1963) described a similar case in which a hydroid grew on the globular colonies of *Fedora nodosa*.

The specimens of *A. parkeri* were accompanied by other rooted species associated with sand-faunas. These included *Parmularia* sp., *Parastichopora vanna* (see Cook & Chimonides, 1981) and *Conescharellina* sp.

Anaskopora doliaris (Maplestone) (Figs 1C,D, 2C,D, 4A,B)

Cellepora doliaris Maplestone, 1909: 272, Pl. 77, Figs 10 A,B.
Reginella doliaris Brown 1958: 53; Hastings 1964: 254, Pl. 1, Figs 1-3, Pls 2 and 3.

LECTOTYPE (indicated here): AMU201, 22 miles (35.4km) East of Port Jackson, New South Wales, 80 fath. (146m), HMCS 'Miner'; labelled 'TYPE'. PARALECTOTYPE: BMNH1909.11.12.14, as above.

MATERIAL EXAMINED. QMG21286, G21287, 'Cidaris 1' Stn 43.2, 17°34.58'S, 146°53.21'E, 15.v.1986, 458-500m, epibenthic sledge (1/2 inch inner liner), 2 colonies on SEM stubs; at MTQ.

DESCRIPTION. Colony conical, one autozooid thick (Fig. 1D), inferred to be anchored by basal rhizoids. Autozooids erect, deeply immersed and oriented with the distal part of the orifice towards the ancestrula and the centre of the colony (Fig. 1C). Each autozooid with a series of simple septulae in the lateral, distal and proximal walls (Fig. 4B), all septulae becoming included in a series of chambered pores which develop frontally into new autozooids or avicularia (Fig. 4B). The budding of autozooids is regular and radial, each astogenetic generation of autozooids alternating with one of kenozooids (Fig. 2C). Autozooid frontal shield with about 25 closely spaced costae, the distal costae thickened as an apertural bar which may be weakly bifid or thickened to form a median ridge (Figs 2C,D). Costae alternate with regular rows of 7-8 fine lacunae on each side of the mid-line. Secondary calcified orifice rounded, with a pair of flattened, curved bifid to trifid oral spines (Fig. 2D), a raised, fimbriated distal plate with 3 denticles (Fig. 4A) and distal pit (Fig. 4A), and a pair of condyles. Avicularia usually paired, oral (Fig. 2C), or single, proximal (Figs 1D, 4B); rostra raised, with paired condyles (Fig. 2C). Basal surface of cone hollow, with large paired foramina surrounded by kenozooids and avicularia budded round the proximal ends of the successive generations of erect autozooids (Fig. 1D).

Colony and zooid dimensions are given in Table 1.

REMARKS. Maplestone (1909) described the colony as encrusting, but there was no sign of any substratum in specimens we examined. Of the 39 species listed by Maplestone (1909) associated with *A. doliaris* from New South Wales, 11 were new to science and 15 had a sand-fauna (see Cook, 1981) adapted colony form. Of these, 10 had rhizoids (7 species of *Conescharellina*, 1 of *Zeuglopora*, 1 of *Sphaeropora*, and 1 of *Anaskopora*), and 5 were free-living, lunulitiform species (1 of *Lunularia*, 3 of *Selenaria* and 1 of *Otionella* spp.).

Hastings (1964) gave a very full description and interpretation of colony growth and relationships in *C. doliaris*. She noted the development of kenozooids from septulae, and figured and described the distal fimbriated plate. However, her account was written before the explanation of frontal budding by Banta (1972) and of reversed frontal budding by Cook & Lagaaij (1976). Hastings used the structure of the ascophoran genus *Conescharellina* in her comparisons. The budding pattern is analogous in the two examples, although the type of frontal bud produced is quite different in *Conescharellina*. Hastings (1964: 258; 1966: 68) noted the similarities in development of intercalated avicularia and kenozooids in *C. doliaris* and *Membraniporella agassizii* Smitt (1873: 11, Pl. 5, Figs 103-106), from Florida. *M. agassizii* is erect and quadriserial; the autozooids have costae without either pelmatidia or lateral costal fusions (see also Ristedt, 1979, Pl. 2, Figs

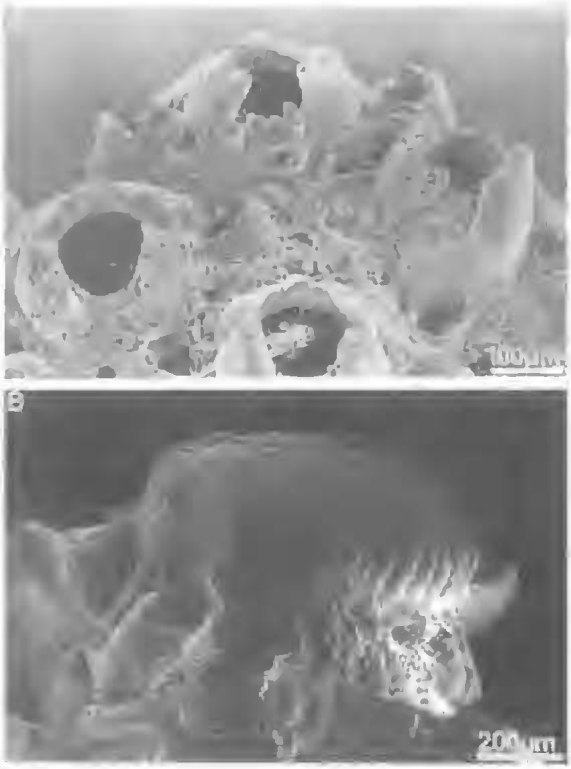

FIG. 4. *Anaskopora doliaris* (Maplestone). A, QMG21286, details of orifices, x 90; B, QMG21287, details of kenozooids, x 55.

1, 2). The gymnoeyst is distinct early in ontogeny, but later changes produce avicularia and kenozooids surrounding the autozooids which eventually obscure all but the orifices on the frontal surface of branches. The origin of the kenozooids and avicularia has not been described, but may be inferred to be from chambered pores similar to those in *Anaskopora*. They appear to strengthen the delicate, erect branches. Hastings (1964) also emphasized the similarities in interzooidal budding from the pore-chambers of *Hippothoa* with the budding of kenozooids in *C. doliaris*. The similarities in pore-chamber and chambered-pore structure are discussed by Bock and Cook (in press).

Anaskopora doliaris is known from only 4 colonies. The lectotype and paralectotype were both from the 'Miner' collections, one specimen having been sent by Maplestone to the then British Museum (Natural History) as a 'cotype'. We infer that the two colonies of *Anaskopora doliaris* from the 'Cidaris 1' collection were anchored by rhizoids like those of *A. parkeri*, which probably emanate from the large, paired foramina on the basal surface (Fig. 2C). It differs from *A. parkeri* and the other globular, fossil species, *A. elevata*, *A. cornuta* and *A. rotundata* (see Bock & Cook, in press), in the regularity of its reversed frontal budding and hollow basal surface. It resembles other species of *Anaskopora* in the mode of development and distribution of interzooidal kenozooids and avicularia, and the presence of distal fimbriated plate in the autozooids. The reasons for its removal from the genus *Reginella* are related to the history of the concepts and the characters of that genus which are discussed below.

Reginella Jullien, 1886

The attribution of *Cellepora doliaris* Maplestone, 1909 to the genus *Reginella* by Hastings (1964) seems to have been the result of a series of misconceptions which have had several repercussions in the later interpretation of Australasian and other cribriomorph species.

Reginella was introduced by Jullien (1886: 605) as a genus of Costulidae (=Cribrilinidae), for *C. furcata* Hincks (1882: 470, Pl. 20, Fig. 5), a Recent species from the coast of British Columbia. No other species was included. Jullien's definition was not based upon the examination of specimens, but was an interpretation of Hincks's description and figure. Canu & Bassler (1929: 243) provided a literal English translation of Jullien's generic description, which mentioned that the frontal shield was composed of '*voluminous ribs much in relief*', and that the '*intercostal furrows traverse entirely the zooecium and separate completely each pair of transverse ribs*'. Pelmatidia were described as decreasing in size from the margin along each costa, and the lacunae were noted as each occupying '*the middle of a calcareous polygonal cell*'. Osburn (1950: 179, Pl. 28, Fig. 3) redescribed *R. furcata* from Californian specimens, and noted that septulae were present, that the brooding zooid orifices were dimorphic, that the large ovicells were punctate and had a median keel, and that the oral spines were often absent. Hastings (1964: 253) also redescribed *R. furcata* from Hincks's British Columbian material and noted that Jullien's '*polygonal cells*' were '*no more than an effect of light and shade*'. There are, however, other discrepancies between Hincks's (1882) description and Jullien's (1886) definition. Hincks emphasized that the costae were only '*slightly raised*', and that the intercostal '*grooves*' were '*shallow*' and were arranged '*radiating to the median line*'.

TABLE 1. Comparative measurements of colony, autozooid and avicularium in *Anaskopora parkeri* and *A. doliaris*. Original measurements calculated from scanning electron micrographs. Width of lacuna in microns; all other measurements in millimetres. The frontal shield length marked by an asterisk is a probable misprint in Hastings (1964). Autozooid length is considered the same as frontal shield width.

	A. doliaris (Hastings 1964)	*A. doliaris* (original)	*A. parkeri* (original)
Colony dimensions	~ 3.5 x 3	2.9 x 3.3	0.5 - 5
Autozooid length	-	1.06, 1.06, 1.08	0.69, 0.72, 0.76, 0.68
Frontal shield length, width	0.1* x 0.5	0.95, 1.01 L, 0.66, 0.70 W	0.49, 0.60 L, 0.41 W
Aperture autozooid	-	0.21, 0.22, 0.22 L, 0.22, 0.24, 0.24 W	0.14, 0.15 L, 0.17, 0.18,0.21 W
Apertural bar width	-	0.15	0.05, 0.07
Lateral oral spine	-	0.3, 0.4, 0.4, 0.4 L, 0.2, 0.2 W	0.1, 0.1 L, 0.06, 0.06 W
Number of denticles on fimbriated plate	2	2-3	5-8
Width of pit at base of fimbriated plate	-	0.07, 0.07, 0.10	0.06
Number of costae	9-13 (one side only)	10-25	18-24
Width of costae	-	0.07, 0.07, 0.09,0.09	0.03, 0.03, 0.03, 0.04, 0.06, 0.06, 0.06, 0.09
Number of lacunae per side	-	5-8	7-8
Width of lacunae	-	9-10	10-25
Height of oral avicularium	-	0.18, 0.19	0.14
Aperture of oral avicularium	-	0.16, 0.16 L, 0.12, 0.10 W	0.17, 0.17, 0.17 L, 0.13, 0.13, 0.13 W
Width of basal kenozooidal chambers	-	0.16, 0.19, 0.29	not applicable

This is in contrast to Jullien's prominent costae, and furrows which traversed the zooid horizontally. Cook (1985: 123) also examined Hincks's specimens of *R. furcata* and noted that the costae were broad and flattened, with pelmatidia and small lacunae, and remarked '*the relationship of* R. furcata *with the various species subsequently assigned to* Reginella *requires investigation*'. The type and other specimens of *R. furcata* have been re-examined, and a short description is given below.

Reginella furcata (Hincks)

Cribrilina furcata Hincks, 1882: 470, Pl. 20, Fig. 5.
Reginella furcata O'Donoghue & O'Donoghue 1926: 52; Osburn 1950: 179, Pl. 28, Fig. 3; Hastings 1964: 253; Soule et al. 1995: 123, Fig. 42 A-C.

MATERIAL EXAMINED. BMNH1886.3.16.18, Queen Charlotte Islands, Hincks Coll. on 4 shell fragments; 1921.11.17.12 and 1968.1.18.100, Departure Bay, Vancouver Island, O'Donoghue Coll; 1986.9.10.3 Cannon Beach, Western Washington, L. Pitt Coll.

DESCRIPTION. Autozooids encrusting, colony originating from a membraniporiform ancestrula with long marginal spines. Zooidal gymnocyst very narrow, vertical walls shallow. Frontal shield of 11-17 flattened costae, each with 3-4 pelmatidia. Suboral bar variously thickened, sometimes with a minute central mucro. Costae irregularly fused with a shallow central suture; the distal pairs of costae extending horizontally, the proximal 5-7 pairs converging distally and medially. Intercostal furrows narrow, with 4-6 rounded lacunae. Six evanescent oral spines, one lateral pair often remaining, and becoming thickened, or extended frontally and bifurcated terminally. Zooids communicating through 2 distal and 3 lateral groups of septulae, each enclosed in a very shallow, slit-like chamber at the base of the gymnocyst. Ovicells large, hyperstomial, with a median suture line and 16-20 small, rounded or irregular pores scattered over the surface; fertile orifices very slightly wider than autozooid orifices. Avicularia absent.

REMARKS. Osburn (1950) illustrated a single zooid of his Californian material of *R. furcata*. The drawing is misleading, as it resembles Jullien's concept of *Reginella* rather more than Hincks's description of *R. furcata*. The zooid appears to be at a late ontogenetic stage, with thickened, but not prominent, costae and the lines of lacunae traverse the frontal shield horizontally, with no obvious median suture line. Pelmatidia were reported to be present but were not

illustrated. Osburn (1950: 180, Pl. 28, Fig. 4 and Pl. 29, Fig. 3) also illustrated another Californian species as *Reginella mucronata*, which had originally been introduced for Pleistocene material from the same region by Canu & Bassler (1923: 92, Pl. 35, Fig. 4). Canu & Bassler (1923) referred it to the genus *Metracolposa* Canu & Bassler (1917). Canu & Bassler's (1923) retouched photographs show zooids very similar to that illustrated by Osburn for *R. furcata*, rather than the rounded zooids with large lacunae he illustrated for *R. mucronata*. Hastings (1964: 253) considered that these two species were identical, although Soule (1959: 46), who had examined both fossil and Recent material, had regarded *R. mucronata* as distinct. The genus *Metracolposa* was originally introduced for the Eocene species *M. robusta* Canu & Bassler (1917: 35, Pl. 3, Fig. 6; and 1920: 308, Pl. 43, Figs 1-7), from North Carolina. *M. robusta* and the other Eocene species described by Canu & Bassler were all illustrated by heavily retouched photographs, many of elongated zooids with uninterrupted lines of lacunae extending across the frontal shield, with little or no indication of a median suture line. *M. robusta* has large, erect, bilaminar colonies and zooids with paired oral avicularia. The ovicells are very large and ridged centrally, but not punctate like those of *R. furcata*. Generally, *M. robusta*, the type species, and the other Eocene forms assigned to *Metracolposa*, have little in common with, and are distinct from, *Reginella*. We accept that the Pleistocene-to-Recent *M. mucronata* is congeneric with *R. furcata*, but this provides no justification for regarding the genus *Metracolposa* as a synonym of *Reginella*. That idea had been very tentatively suggested by Osburn (1950) but was later greatly extended by Hastings (1964) in order to include other species with avicularia within the generic description (see below).

Jullien's (1886) definition and the studies just cited so modified the generic concept of *Reginella* that it now included characters quite unlike those of its type species. This would explain the implicit referral of *Cribrilina vas* Brown, 1954, a Pliocene species from New Zealand, to *Reginella* by Brown (1958), when discussing a somewhat similar species from the Tertiary of Victoria, *Reginella maplestonei* Brown, 1958. Neither species has avicularia, but small, peristomial ovicells were illustrated in *R. maplestonei*. Powell (1967: 221, Pl. 2, Fig. 6, Fig. 4) redescribed *R. vas* from Recent New Zealand specimens, noting its elongated zooids, absence of pelmatidia, and small, imperforate, peristomial ovicells; all characters completely unlike those of *R. furcata*. Brown (1958) also included the Recent, Antarctic *Cribrilina projecta* Waters, 1904, which has small oral avicularia and distinct pelmatidia, in his concept of *Reginella*. Hastings (1964) considered that *C. projecta* was not congeneric with *R. furcata*, but gave no evidence for her conclusion. Moyano (1985) introduced the genus *Dendroperistoma* for *C. projecta*.

The characters of *Cellepora doliaris* Maplestone, 1909 also became involved in the *Reginella* problem, when Brown (1958:53) mentioned that Hastings (presumably in litt.), '*has also pointed out a very close resemblance in the nature of the frontal shield between* C. vas *and* Cellepora doliaris *Maplestone*'. Hastings, however, did not redescribe *C. doliaris* for a further 6 years. When she did, she remarked (1964: 258, footnote 1), with a reference to Brown (1958), that Brown had told her in 1955 that he had '*referred* Cribrilina alcicornis *and* Cellepora doliaris *to* Reginella' when, in fact, Brown (1958) had never mentioned *C. alcicornis* at all (see below).

C. alcicornis Jullien (1883: 508, Pl. 14, Figs 23-25) is a deep-water, encrusting species from the Northeastern Atlantic. Autozooids have costae with no pelmatidia, and four, large, branched oral spines. Interzooidal avicularia and large interzooidal kenozooids are budded among the autozooids, and the elongated ovicells are not punctate. *C. alcicornis* is therefore unlike *R. furcata*, and it is significant that Jullien (1886) did not include *C. alcicornis* when introducing *Reginella*, and that later, Calvet (1907:399) and Prenant & Bobin (1966: 578, Fig. 200), continued to refer the species to *Cribrilina*. More recently, both d'Hondt (1974: 47, Fig. 7) and Harmelin (1978: 178, Pl. 1, Fig. 3, Figs 3-4), who examined additional Atlantic material, also maintained *C. alcicornis* in *Cribrilina*. Harmelin noted that one of Hastings's '*points of resemblance*' between *C. doliaris* and *C. alcicornis* was based on the mistaken assumption that Jullien's (1886) phrase '*grande ponctuations*' referred to the interzooidal kenozooids, whereas in fact, it referred to the intercostal lacunae. He remarked '*Le changement de genera ne semble pas justifié pour cette espèce*'.

Quite apart from this confusion, it is unfortunate that Hastings (1964: 252) extended Osburn's (1950) tentative synonymy of *Metracolposa* with *Reginella*, including some of the characters of the Eocene *M. robusta*, such as avicularia, in her

concept of *Reginella*. Thus the presence of numerous avicularia in *C. doliaris*, which are totally absent in *R. furcata*, did not preclude its referral to *Reginella*, because avicularia had become a 'generic character'. In the same way, the presence of kenozooids with the avicularia in *C. doliaris*, was mitigated by the tacit assignment of *Cribrilina alcicornis*, which has both, to *Reginella*, although neither were present in *R. furcata*. The presence of avicularia and kenozooids in both *C. alcicornis* and *C. doliaris* is interesting, but the structures differ completely in their origins and general morphology between the two species. In any case, neither has anything to do with the characters of the genus *Reginella*. Two North American species which have been referred to *Reginella* also require further investigation. *Reginella floridana* (Smitt, 1873) has been described by Winston (1982) from Florida, and by Cook (1985) from West Africa. No ovicells have ever been found in any specimen of this species. *R. repangulata* Winston & Håkansson, 1986, from an interstitial Floridan fauna, has ovicells somewhat similar to those of *R. furcata*.

It is obvious that by this time the original characteristics of the genus have become completely submerged by the accumulation of additional or alternative features derived from the diversity of species included. This is illustrated by Gordon (1984: 63, Pl. 20, Figs D-E), who redescribed *Reginella vas*, and introduced a new, uniserial encrusting species from New Zealand, *R. stolonifera* Gordon (1984: 63, Pl. 20, Figs A-C), which had large, branched oral spines like those of *C. alcicornis*. The concept of the genus was now extended to include all the disparate forms mentioned above, from the Arctic, Antarctic, Atlantic and Pacific Oceans, from deep and shallow, even interstitial waters, and from the Tertiaries of North America, Australia and New Zealand. The generic characters now encompassed: colonies encrusting, erect and bilaminar, and conical; zooids uniserial to contiguous and frontally budded; avicularia present or absent; ovicells hyperstomial and peristomial with or without pores or fenestrae; pore chambers present or absent. To these may be added, pelmatidia and kenozooids present or absent. The only consistent characters are 'slit-like intercostal lacunae', and 'costae arranged in straight rows across the zooid, often traversing the mid-line without interruption'. Although these features occur late in ontogeny in *R. vas* and *R. stolonifera*, neither occurs in *R. furcata*.

In conclusion, it is obvious that *Reginella* should be restricted to Recent and Pleistocene species from the North American and Japanese Pacific coasts, and that *Metracolposa* should be retained only for the American Eocene species. Soule, Soule & Chaney (1995) give notes on *Reginella furcata* and introduce a new genus, *Reginelloides*, for *R. stolonifera* Gordon, 1984. *Cribrilina alcicornis*, *C. vas*, *Reginella maplestonei*, *R. floridana* and *R. repangulata* should also be re-investigated, and new generic groups should be introduced for their reception where necessary.

The colonies of *R. furcata* from Vancouver Island examined by one of us (PLC) included about 20 with ancestrulae present. The ancestrulae had small pore-chambers distally and laterally, and 12 long spines surrounded the opesia. Mawatari (1988: 149, Figs 9-14) has described specimens from Hokkaido, Japan, as *Reginella furcata*, and discussed previous Japanese records in detail. These include the species described as *Lyrula multipora* by Sakakura (1935: 109, Pl. 8, Fig. 7), and as *Figularia multipora* by Silén (1941: 117, Figs 178-180). All these Japanese records differ from *R. furcata* very slightly, in the complete lack of oral spines, even in early ontogeny, the raised mucros beside the orifice which give it a subtriangular appearance, and the lack of any dimorphism in the fertile orifices. Osburn (1950) described several nominal taxa from the Arctic to the Mexican coasts of North America and referred them to *Reginella*. They all resemble *R. furcata* in possessing straight, converging rows of lacunae, paired oral spines and large ovicells with a central suture and punctate surface. Until the actual limits of variation of these species, especially those from California, like *R. macronata*, have been analysed, it is probably best to maintain them, together with *R. multipora*, as distinct species of *Reginella*.

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